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ABSTRACT: Our objectives were to determine the influences of supplemental nonprotein N or protein on feed intake, digestibility, and postabsorptive N metabolism in sheep fed a high-concentrate diet for ad libitum consumption. Nine Romanov-sired, crossbred wethers (13 mo old; 52 kg) were fitted with catheters in a mesenteric artery, mesenteric vein, portal vein, and hepatic vein. Wethers consumed a 95% concentrate diet ad libitum. Treatments consisted of control (no supplemental N; 6.6% CP) or supplemental urea (11.4% CP), soybean meal (SBM; 11.2% CP) or ruminally undegradable protein (BFM; 11.2% CP; 50:50 blood meal and feather meal). Intake or apparently digested intake of DM, OM, and energy did not differ between control and N-supplemented ($P > 0.40$), or between urea- and protein-supplemented ($P > 0.40$), but were greater ($P < 0.05$) in SBM- than in BFM-supplemented wethers. Intake and apparently digested intake of N were less ($P < 0.01$) in wethers fed the control diet than in those receiving N supplementation but were less ($P = 0.03$) in BFM- than in SBM-supplemented wethers. Neither portal nor hepatic venous blood flows differed ($P > 0.15$) among treatments. Net portal release and hepatic uptake of α-amino N and ammonia N and hepatic release of urea N were greater ($P < 0.05$) in wethers supplemented with N than in controls, but portal-drained viscera (PDV) uptake of urea N did not differ ($P > 0.40$) among diets. Splanchnic release of α-amino N and ammonia N did not differ from 0 or among diets ($P > 0.10$), but net release of urea N was less ($P = 0.05$) for control than for sheep receiving N supplementation. No differences ($P > 0.10$) in blood concentration within vessel or net flux across PDV, hepatic, or splanchnic tissues of α-amino N, ammonia N, or urea N were observed among wethers receiving supplemental N. Net uptake of oxygen by the PDV did not differ among diets, but hepatic uptake was less ($P < 0.05$) in control and urea-supplemented sheep than in sheep receiving SBM or BFM. These observations suggest that the source of supplemental N had no large effects on the overall N economy of the animals used in this study.

Key Words: Maize, Protein Digestibility, Rumen Digestion, Soybean Oilmeal, Urea, Wethers

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Introduction

Ruminants recycle substantial amounts of N as urea by transfer from blood to the gut. Recycled N is potentially of substantial importance to the total N economy in ruminants, especially when dietary N is low. However, the significant and variable amounts of recycled N impose major problems on the estimation of the dietary N requirements of the animal. Estimation of dietary amino acid requirements of ruminants is even more complex because of the variable contribution of amino acids of microbial as well as of dietary origin to the amino acid supply. Large differences exist among protein sources in the extent to which they escape microbial degradation in the rumen and vary to an even greater extent in the quantities of individual amino acids supplied to the small intestine (Titgemeyer, 1989). Influences of ruminally undegraded protein sources on amino acid supply to the small intestine and disappearance from the intestine have been studied extensively, but less is known regarding impacts of N source on amino acid absorption and subsequent postabsorptive N metabolism. Ferrell et al. (1999) observed that the source of N had little effect in mature wethers consuming low-quality bromegrass hay. Different responses to supplementation of high-concentrate diets are likely, but only limited data are available. Huntington (1989) reported that increased intake of readily fermentable carbohydrate reduced hepatic urea synthesis but increased the proportion recycled to the

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Table 1. Composition of diets fed to sheep

Ingredient	Diet			
	Control	Urea	SBM	BFM
Dry rolled corn	80.00	80.00	80.00	80.00
Chopped brome hay	5.00	5.00	5.00	5.00
Soybean oil	3.00	3.00	3.00	3.00
Limestone	1.00	1.00	1.00	1.00
Potassium chloride	0.35	0.35	0.35	0.35
Sodium chloride	0.30	0.30	0.30	0.30
Dicalcium phosphate	0.15	0.15	0.15	0.15
Trace mineral premix[a]	0.05	0.05	0.05	0.05
Vitamin A, D, E premix[b]	0.05	0.05	0.05	0.05
Vitamin E premix[c]	0.05	0.05	0.05	0.05
Elemental sulfur	0.05	0.05	0.05	0.05
Rumensin-60[d]	0.008	0.008	0.008	0.008
Cornstarch	10.00	8.36	0.42	4.80
Urea		1.64		
Soybean meal, 49% CP			9.58	
Blood meal				2.60
Feather meal				2.60
Laboratory analyses				
DM, % of diet	89.3	89.6	90.0	89.1
OM, % of DM	96.7	96.8	95.9	95.8
CP, % of DM	6.6	11.4	11.2	11.2

[a]Contained 14% Ca, 12% Zn, 8% Mn, 10% Fe, 0.2% I, and 0.1% Co.
[b]Each gram of premix contained 8,800 IU of vitamin A, 880 IU of vitamin D, and 0.88 IU of vitamin E.
[c]Each gram of premix contained 44 IU of vitamin E.
[d]Each gram contained 147 mg of monensin; used under veterinary prescription as a coccidiostat.

portal-drained viscera (**PDV**). However, in a subsequent study, Huntington et al. (1996) observed that with equal N and ME intake, liver urea N release increased, urinary urea N increased, and urea N recycled to the PDV tended to decrease. The objective of this study was to determine influences of supplemental urea and protein on feed intake, digestibility, and postabsorptive N metabolism in sheep fed a high-concentrate diet for ad libitum consumption.

Materials and Methods

Sheep. The experiment was approved by the U.S. Meat Animal Research Center's Animal Care and Use Committee. The nine Romanov-sired, crossbred wethers were 13 mo old and weighed 51.7 kg BW (range 46.8 to 61.2) at the start of the experiment. Wethers were surgically fitted with indwelling catheters placed in a mesenteric artery, mesenteric vein, portal vein, and hepatic vein as described previously (Ferrell et al., 1991). The catheters were placed in the sheep when they were 6 mo old. They were used in a previous experiment and fed high-forage diets until this experiment began. Arterial and portal venous catheters were patent in nine sheep, but the hepatic venous catheter was patent in only six sheep.

Experimental Design. The nine wethers were used in a Latin square design consisting of four diets and four sampling periods. Wethers were offered total mixed diets ad libitum (Table 1). Dietary treatments consisted of no supplemental N (control), supplemental N as urea, supplemental protein as soybean meal (**SBM**), or ruminally undegradable protein (**BFM**). Ruminally undegradable protein was a 50:50 mixture of blood meal and feather meal. Diets were formulated so that urea or protein was added to increase the CP of the diets by 4.7 percentage units as compared with the control. Protein was substituted for cornstarch, so that corn protein and hay protein were similar across diets. Monensin was included in the diets by veterinary prescription to prevent coccidiosis.

Housing, Feeding, and Sampling. Wethers were placed in individual elevated pens (1.2 m^2) equipped with wire mesh floors (0.63 × 3.5-cm slots). The room had a 12-h light-dark cycle (light 0700 to 1900), and temperature was maintained at 20°C. Sheep were fed once daily at 0900. The amount of feed offered was from 105 to 120% of the previous 3-d average intake. At 0700, orts were removed, weighed, and refed with the new daily feed. Sheep were without feed from 0700 to 0900. Feeding the orts from the previous day was an attempt to ensure that the complete diet offered was consumed.

Each of the four sampling periods consisted of 21 d. Days 1 through 13 were for diet adaptation. On d 14, sheep were fitted with harnesses and fecal bags for total fecal collection on d 14 through 19. Feces were collected between 0730 and 0900, weighed, subsampled (10%), and stored at 2°C. At the end of each period, subsamples were composited and stored frozen (–20°C). Blood sampling was undertaken on four sheep on d 20 and five sheep on d 21. During blood sampling, sheep were placed in portable crates (40 × 117 cm) at 0700. Water was provided, and the feeding protocol was similar to that described above. A primed (15 mL), continuous infusion (0.6 mL/min) of para-aminohippuric acid (**PAH**, 4% wt/vol) into the mesenteric venous catheter was begun at 0730. Ten milliliters of blood was drawn in heparinized tubes simultaneously from the mesenteric arterial, portal venous, and hepatic venous catheters at 0800, 0820, 0840, and 0900 and then at hourly intervals for 6 h. Four samples were taken before feeding to establish a prefeeding base, and six were taken postfeeding. These sampling times were chosen to provide a basis for inference to a 24-h day. Samples of blood were placed on ice immediately. An additional sample of blood from each vessel was drawn into a heparinized 1-mL syringe, placed on ice, and analyzed within 10 min for hemoglobin and percentage oxygen saturation of hemoglobin (Hemoximeter, model OSM 1, Radiometer, Copenhagen). Oxygen concentrations in blood were calculated as described by Burrin et al. (1991). At 1600 on d 21, a sample of ruminal contents (25 mL) was collected from each sheep via stomach tube. This time was chosen to minimize handling of the sheep and potential interference with digestion studies and blood flow-net flux measurements. Each sample of ruminal contents was acidified (2 mL of 20% vol/vol; HCl added to 8 mL of ruminal contents), and then frozen (–20°C) for storage.

Laboratory Analyses. Dry matter of feed and feces were determined by drying in a forced-air oven at 60°C for 48

h. Samples were ground (1 mm screen) by use of a Wiley Mill and then assayed for ash (AOAC, 1975), N (AOAC, 1976), and energy (bomb calorimetry). Within 2 h of sampling, whole blood was assayed for PAH, α-amino N, ammonia N, and urea N, and blood flows and net nutrient flux were calculated (Ferrell et al., 1999). Concentrations of ammonia N in ruminal fluid were determined as described previously (Ferrell et al., 1999).

Statistical Analyses. Data on feed intake and nutrient digestibility were analyzed by analysis of variance using GLM procedures of SAS (SAS Inst. Inc., Cary, NC). The model included dietary treatment, period, and sheep. Three single-degree of freedom comparisons were made to evaluate supplement effects: 1) control vs N-supplemented, 2) nonprotein N (urea) vs protein (SBM and BFM) supplementation, and 3) ruminally degradable protein (SBM) vs BFM. Metabolite concentrations in whole blood, blood flow, and net flux of metabolites across the portal-drained viscera (PDV) and liver were averaged across hour within sheep and sampling day. The resulting means were analyzed by analysis of variance as described for the feed intake and nutrient digestibility data.

Results

Intake and Digestibility. As designed, the N intake of wethers when fed the control diet was less ($P < 0.001$) than N intake of wethers fed the N supplemented diets (Table 2). Nitrogen intake of wethers fed the diet containing urea was not different ($P = 0.43$) from that of protein-supplemented diets, but N intake was greater ($P = 0.03$) with SBM than with BFM as the protein source. Neither DM, OM, nor gross energy intakes of the control diet differed ($P > 0.60$) from intakes of diets containing N supplements, nor did they differ ($P > 0.40$) between diets containing urea and diets containing protein. Dry matter ($P = 0.02$), OM ($P = 0.02$), and energy ($P = 0.04$) intakes of the diet containing SBM was greater than those of the diet containing BFM as the supplemental protein source.

Fecal output of N did not differ ($P > 0.10$) among dietary treatments. Fecal output of energy (P = 0.04) was greater and fecal DM and OM tended ($P = 0.07$) to be greater for wethers consuming the urea-containing diet compared with SBM- and BFM-containing diets. Fecal output of DM, OM, and energy by wethers fed the control diet was intermediate between observed values for urea- and protein-supplemented diets.

Apparent digestibility of N of the control diet was less ($P < 0.01$) than for diets containing N supplements. No differences in apparent digestibility of N ($P > 0.26$) attributable to N source were observed. However, apparent digestibility of energy was less ($P = 0.03$) and digestibility of DM and OM tended ($P \leq 0.10$) to be less for the urea- than for SBM- and BFM-supplemented diets.

As a result of lower N intake and lower apparent digestibility, the total apparently digested intake of N by wethers fed the control diet (6.95 g/d) was much less ($P < 0.001$) than that of wethers fed N-supplemented

Table 2. Influence of dietary supplementation on intake and digestibility of high-concentrate diets by sheep

	Diet[a]						Contrast[b]		
Item	Control	Urea	SBM	BFM	$\bar{x}$	SE	1	2	3
No. observations	9	9	9	9					
Body weight, kg	57	57	58	58	57.6	0.40	0.57	0.34	0.77
Intake									
DM, g/d	1,096	1,134	1,186	1,011	1,107	31.5	0.80	0.57	0.02
OM, g/d	1,059	1,098	1,138	968	1,066	30.3	0.88	0.45	0.02
N, g/d	11.6	20.6	21.3	18.2	17.9	0.58	0.01	0.43	0.03
Energy, kcal/d	4,893	5,065	5,349	4,637	4,986	142.0	0.64	0.80	0.04
Fecal Output									
DM, g/d	193	204	188	155	185	8.8	0.52	0.07	0.11
OM, g/d	172	181	164	138	164	8.1	0.45	0.07	0.16
N, g/d	4.61	5.48	5.26	5.01	5.09	0.22	0.13	0.42	0.62
Energy, kcal/d	904	972	874	737	871	39.5	0.56	0.04	0.14
Apparent digestibility, %									
DM	82.5	82.2	84.2	84.7	83.4	0.63	0.30	0.08	0.72
OM	83.8	83.7	85.6	85.8	84.7	0.61	0.27	0.10	0.89
N	59.9	73.7	75.4	72.5	70.4	1.12	0.01	0.90	0.26
Energy	81.6	80.9	83.7	84.1	82.6	0.66	0.10	0.03	0.78
Apparently digested intake									
DM, g/d	903	931	998	856	922	26.3	0.60	0.94	0.03
OM, g/d	887	916	974	831	902	25.6	0.67	0.77	0.02
N, g/d	6.95	15.14	16.00	13.18	12.8	0.46	0.01	0.54	0.01
Energy, kcal/d	3,989	4,094	4,476	3,900	4,115	120.4	0.46	0.69	0.05

[a]Diets were control (no supplemental N), urea added as a N source, soybean meal (SBM) added as an intact soluble protein source, and ruminally undegradable protein (BFM; 50% blood meal, 50% feather meal).
[b]Contrasts were 1) control vs N supplemented (urea, SBM, BFM), 2) nonprotein N (urea) vs intact protein (SBM, BFM), and 3) degradable (SBM) vs undegradable (BFM) protein. Probability that values were not different are shown.

Table 3. Influence of dietary supplementation on blood flow and net nutrient flux across portal-drained viscera and hepatic tissues of sheep fed a high-concentrate diet

	Diet[a]						Contrast[b]		
Item	Control	Urea	SBM	BFM	x̄	SE	1	2	3
Blood flow, L/h									
Portal venous	125	118	127	126	124	3.43	0.90	0.24	0.98
Hepatic venous	153	146	153	163	154	4.51	0.89	0.16	0.28
Hepatic arterial	17	21	27	25	23	2.50	0.09	0.26	0.62
α-Amino-N concentration, m*M*									
Artery	5.05	4.65	4.69	4.85	4.81	0.086	0.06	0.47	0.42
Portal vein	5.29	4.93	4.99	5.19	5.10	0.096	0.18	0.40	0.36
Hepatic vein	5.04	4.82	4.69	4.92	4.87	0.102	0.18	0.91	0.28
α-Amino-N net release, mmol/h									
PDV[c]	29.2	33.3	37.6	44.2	36.1	2.37	0.05	0.12	0.23
Hepatic	–28.9	–36.0	–38.1	–47.7	–37.7	3.30	0.05	0.25	0.17
Splanchnic	3.17	0.80	2.95	5.39	3.08	4.01	0.99	0.63	0.76
Ammonia-N concentration, m*M*									
Artery	0.172	0.162	0.164	0.176	0.169	0.005	0.64	0.43	0.31
Portal vein	0.230	0.274	0.256	0.270	0.258	0.006	0.01	0.38	0.33
Hepatic vein	0.169	0.158	0.159	0.177	0.166	0.007	0.66	0.39	0.22
Ammonia-N net release, mmol/h									
PDV	6.47	12.8	11.7	11.8	10.7	0.614	0.01	0.40	0.92
Hepatic	–7.78	–13.7	–13.3	–15.2	–12.5	0.756	0.01	0.69	0.22
Splanchnic	–1.31	–1.40	–1.39	–2.28	–1.59	0.275	0.41	0.37	0.13
Urea N concentration, m*M*									
Artery	4.00	7.75	9.38	8.25	7.34	0.365	0.01	0.16	0.19
Portal vein	3.82	7.54	9.18	8.06	7.15	0.360	0.01	0.15	0.19
Hepatic vein	3.70	8.22	9.75	8.64	7.58	0.580	0.01	0.35	0.35
Urea N net release, mmol/h									
PDV[c]	–23.3	–24.7	–26.2	–26.8	–25.3	1.74	0.43	0.62	0.89
Hepatic	37.4	52.3	55.2	68.3	53.3	3.83	0.01	0.18	0.11
Splanchnic	11.2	23.9	26.7	34.0	24.0	2.94	0.01	0.23	0.23
Oxygen concentration, m*M*									
Artery	5.72	5.54	5.46	5.65	5.59	0.069	0.21	0.93	0.24
Portal vein	4.40	4.31	4.22	4.42	4.34	0.078	0.57	0.91	0.27
Hepatic vein	3.33	3.13	3.02	3.07	3.14	0.123	0.21	0.68	0.84
Oxygen net uptake, mmol/h									
PDV[c]	163	145	155	157	155	4.94	0.28	0.28	0.87
Hepatic	178	185	229	239	208	9.38	0.03	0.01	0.61
Splanchnic	353	341	391	411	374	13.45	0.23	0.03	0.46

[a]Diets were control (no supplemental N), urea added as a N source, soybean meal (SBM) added as an intact soluble protein source, and ruminally undegradable protein (BFM; 50% blood meal, 50% feather meal).
[b]Contrasts were 1) control vs N supplemented (urea, SBM, BFM), 2) NPN (urea) vs intact protein (SBM, BFM), and 3) degradable (SBM) vs undegradable (BFM) protein. Probability that values were not different are shown.
[c]PDV: portal-drained viscera.

diets (14.8 g/d). The lack of differences in intake and apparent digestibility of N between urea- and protein-supplemented diets resulted in similar apparently digested N (15.1 and 14.6 g/d). Total apparently digested N by wethers fed the SBM (16.0 g/d) diet was greater ($P < 0.01$) than by those fed the BFM (13.2 g/d) diet, primarily because of lower intakes by wethers fed the BFM diet. Total DM, OM, and energy apparently digested by wethers fed the control diet did not differ ($P > 0.40$) from those fed diets supplemented with N. Similarly, total digested DM, OM, and energy did not differ ($P > 0.50$) between wethers fed urea and those fed protein-supplemented diets (SBM, BFM) but were greater ($P < 0.05$) for wethers fed SBM than for those fed BFM as the protein source.

Neither hepatic venous nor portal venous blood flow differed ($P > 0.10$) among dietary treatments (Table 3), but hepatic arterial blood flow tended ($P = 0.09$) to be less in control than in N-supplemented wethers. Arterial concentration of α-amino N tended to be greater ($P = 0.06$) in wethers fed the control diet than in those fed diets containing supplemental N. Concentrations of α-amino N in portal and hepatic venous blood followed similar patterns, but differences did not approach significance ($P = 0.18$). In contrast, net release of α-amino N from the PDV and uptake by the liver was less ($P = 0.05$) in control-fed wethers than in wethers fed diets containing supplemental N, which did not differ ($P > 0.10$). Because net release of α-amino N from the PDV was similar in magnitude to uptake by the liver, net splanchnic release of α-amino N did not differ among treatment groups ($P > 0.60$) and did not differ from zero.

Ammonia N concentrations were lower ($P = 0.01$) in portal venous blood of wethers fed the control diet than

in wethers fed diets containing supplemental N. No other differences ($P > 0.20$) in ammonia N concentration were observed. Release of ammonia N from the PDV and uptake by the liver was lower ($P = 0.01$) in wethers fed the control diet than in wethers fed diets containing supplemental N, but no significant differences ($P > 0.20$) between N sources were observed. Net flux of ammonia N across splanchnic tissues did not differ ($P > 0.10$) among diets.

Urea N concentrations in arterial, portal venous, and hepatic venous blood were substantially lower ($P = 0.01$) in control than in N-supplemented wethers, but no significant differences ($P > 0.10$) among N sources were observed. Net uptake (negative release) of urea N by the PDV from blood did not differ ($P > 0.40$) among dietary treatments, even though both net hepatic ($P = 0.01$) and splanchnic ($P = 0.01$) release were nearly twofold greater in N-supplemented wethers than in controls. No significant differences ($P > 0.10$) in hepatic release of urea N were observed between urea- and protein-supplemented wethers, but hepatic release of urea N was numerically greater in wethers fed BFM (34.2 mmol/h) than in those fed SBM (27.6 mmol/h) or urea (26.2 mmol/h).

Concentration of oxygen in arterial, portal venous, and hepatic venous blood did not differ ($P > 0.20$) among dietary treatments. Oxygen uptake by the PDV did not differ ($P > 0.20$) among treatments, but oxygen uptake by the liver of control-fed sheep was less ($P < 0.03$) than in N-supplemented sheep and was lower in urea-supplemented sheep than in protein-supplemented sheep. Hepatic oxygen uptake in SBM- and BFM-fed sheep did not differ ($P = 0.61$). Oxygen uptake by splanchnic tissues in sheep fed the urea-containing diet was less ($P = 0.03$) than in those fed intact protein (SBM or BFM).

Discussion

Intake of dietary N of wethers fed the control diet was less than intake of N by wethers fed diets containing supplemental N, as planned. The control diet also had lower apparent digestibility of N and less total digested N than N-supplemented diets. Metabolic fecal N, calculated as 5.35 g/kg DMI (NRC, 1985), was 5.86 g/d for the control group; however, total fecal N excretion was only 4.61 g/d. This calculation also resulted in metabolic fecal N estimates greater than observed total fecal N for wethers fed urea (6.07 g/d), SBM (6.35 g/d), and BFM (5.41 g/d). An alternative calculation of metabolic fecal protein is 0.068 per unit of indigestible DMI (NRC, 1985). If one assumes indigestible DMI is approximately equivalent to apparently undigested DM, the resulting estimate of metabolic fecal N was 2.10 g/d, or 18.1% of N intake of wethers fed the control diet. In comparison, this calculation results in estimates of metabolic fecal N of 2.22, 2.05, and 1.69 g/d or 10.8, 9.6, and 9.3% of N intake for wethers fed the urea, SBM, and BFM diets, respectively. These estimates suggest that metabolic fecal N has an inordinate effect on estimates of apparent digestibility of N when dietary N concentration and intake N are low. This observation is consistent with those reported previously (Ferrell et al., 1999) with reference to low-quality forage diets.

When high-forage diets are fed, ruminal degradation of SBM protein ranges from about 75 to 85% (Loerch et al., 1983a; Cleale et al., 1987). When included as part of a high-concentrate diet, however, 40 to 50% ruminal degradability of SBM protein may be more typical (Loerch et al., 1983b; Zinn and Owens, 1983). In the present study, ammonia N concentrations in samples of rumen contents were 2.1, 10.2, 2.8, and 2.9 ($\pm$ 1.7) m*M* for control, urea-, SBM-, and BFM-fed sheep, respectively. Although these values should be cautiously interpreted because they were from single samples taken via stomach tube, the pattern observed was consistent with ammonia N concentrations in the portal vein. The low values for control and BFM-supplemented lambs were expected, as was the relatively high value for urea; however, the low value for SBM was somewhat unexpected. We hypothesize that SBM supplementation provided soluble N that was utilized in the rumen to enhance microbial growth, digestion, and intake as well as providing a reasonably high-quality source of amino acids at the intestine. The BFM supplement likely provided a high-quality source of amino acids at the intestine, but amounts of soluble N in the rumen were likely reduced. The BFM supplement resulted in diminished intake and, as a result, reduced digested nutrients compared with SBM. Conversely, urea supplementation resulted in greater amounts of soluble N in the rumen and possibly increased microbial growth but provided less high quality, dietary protein at the intestine compared with the SBM-supplemented diet. The net result was that energy available to the animal (apparently digested energy) was very similar in control, urea-, and BFM-supplemented lambs, although via different mechanisms. These hypotheses are consistent with observed patterns of net α-amino N release from the PDV. It is also important to note that, as a result of reduced intake and(or) high digestibility, fecal losses of DM, OM, and energy were reduced in protein-supplemented compared with control and urea-supplemented lambs. This was especially evident in BFM-supplemented lambs, in which fecal losses of DM, OM, and energy were reduced about 24% as compared with urea-supplemented lambs.

The net release of α-amino N from the PDV averaged 36 mmol/h, and differences among dietary treatments followed expected patterns. Hepatic uptake, however, paralleled PDV release, resulting in small, positive net splanchnic release that was not statistically different from zero. The mean splanchnic net release of α-amino N in the present study was 3.08 mmol/h, or about 1.04 g/d. Average daily gain of lambs in this study was 0.18 $\pm$ 0.09 (means $\pm$ SD) kg/d. Typical N accretion rates in the empty body of lambs growing at 0.25 kg/d is about 5 g/d (Ferrell et al., 1979). Release from the liver of amino acid N other than as free amino acids may help explain this discrepancy. However, the observation that net splanchnic release was near zero on high-concentrate

diets is consistent with previous reports in sheep. Burrin et al. (1991) reported that, in sheep fed an 80% concentrate diet ad libitum, net splanchnic release of α-amino N was negative, and we reported (Ferrell et al., 1999) that net splanchnic flux of α-amino N was slightly negative in sheep consuming forage diets ad libitum. In contrast, less than half of the PDV release of α-amino N was taken up by the liver in lactating dairy cows fed ad libitum (Reynolds et al., 1988) and positive in lactating ewes (Freetly and Ferrell, 1999). In limit-fed steers, hepatic uptake of α-amino N varied between 50 and 90% of PDV release (Eisemann and Nienaber, 1990; Reynolds and Tyrrell, 1991; Harmon et al., 1993).

The greater net PDV release of ammonia N in sheep fed urea than in sheep fed the control diet was likely a result of greater N intake and greater ruminal ammonia N concentration. Observations that PDV ammonia N release when SBM or BFM was fed were similar to that observed when urea was fed, even though ruminal ammonia N concentrations were similar to controls, suggest that ammonia N production by the gut tissue itself was elevated and(or) that ammonia N production within the lumen of the hindgut was elevated when SBM or BFM was fed. Ammonia N produced by gut tissue would likely occur by metabolism of amino acids (Newsholme and Leech, 1984). Degradation of amino acids consumed in excess of requirements takes precedence over degradation of carbohydrates and fat (Krebs, 1972). The gut probably used amino acids as an oxidative fuel to a greater extent in lambs fed SBM or BFM compared with those fed the control diet. In addition, greater amounts of protein flowing to the hindgut when SBM or BFM was fed would result in greater microbial proteolysis in the hindgut, liberating more ammonia N.

The potential value of reutilization of nitrogen compounds by the ruminant has been discussed in detail by Egan et al. (1986), among others. In this study, uptake of urea N from the blood by the PDV was about 67.5% of intake N for wethers fed the control diet and about 43.7% of intake N for supplemented wethers. These values are similar to those reported by Huntington et al. (1996). These observations suggest that N recycled to the PDV is potentially of substantial importance to the total N economy in ruminants fed high-concentrate diets, and recycled N may be of even greater importance when dietary concentration of N is low. In addition, the significant and variable amounts of "waste products of N metabolism" that appear to be salvaged for further use, impose major problems on the estimation of the dietary N requirements of the animal.

Egan et al. (1986) indicated that 50% of the 40 g/d urea synthesized entered the gastrointestinal tract. Of the 20 g, 3 g entered in saliva, bile, and pancreatic juice, and 16 g entered across the wall of the tract, 10 g of which entered the forestomach. Consistent with those observations, Huntington (1989) indicated that approximately 80% of the N recycled to the PDV in cattle results from direct transfer from arterial blood, with the remaining 20% resulting from transfer via saliva. In the present study, mean urea N release from the liver was 17.9 g/d (38.4 g urea/d) and PDV uptake of urea N was 8.5 g/d (18.2 g urea). Net PDV uptake of urea N from the blood was 47.4% of hepatic release. These values are in close agreement to that of Varady, as cited by Egan et al. (1986), and demonstrate that a large proportion of the waste product of N metabolism is potentially useful to the ruminant. Urea N uptake by the PDV was 62.3, 47.2, 47.5, and 39.2% of hepatic release for control, urea, SBM, and BFM diets, respectively, suggesting large effects of level and(or) source of supplemental N on the proportion of urea released from the liver that was recycled to the PDV.

Although PDV uptake of urea N as a proportion of dietary N intake or hepatic urea N release seemed to differ among treatments, net transfer of urea N to the PDV from blood did not differ ($P > 0.40$) among dietary treatments. Kennedy and Milligan (1980) suggested that transfer of blood urea to the rumen is affected primarily by 1) ruminal ammonia N concentration, 2) blood urea N concentration, and 3) the amount of OM fermented in the rumen. Ruminal ammonia N concentrations suggested that substantial differences existed among dietary treatments. Arterial urea N concentrations differed among dietary treatments over twofold in the present study, but apparent OM digestibility did not differ substantially among diets in this study.

The present findings do not support the conclusions of Kennedy and Milligan (1980), but their conclusions were based primarily on forage diets, whereas the present study was limited to high-concentrate diets. Arterial and ruminal ammonia concentrations were generally lower and digested OM was considerably greater in the present study than in studies cited by Kennedy and Milligan (1980). Net PDV uptake of urea N in the present study was comparable to the maximum transfer to the rumen reported by Kennedy and Milligan (1980). Values observed in the present study were also considerably greater than PDV uptake of urea N observed by Freetly and Ferrell (1998) or Krehbiel et al. (1998) in ewes fed primarily forage diets. Values observed in the present study were similar to those reported previously (Ferrell et al., 1999) for lambs fed a low-quality forage diet supplemented with energy (cornstarch and molasses) plus urea or soybean meal, but greater than observed in unsupplemented diets, or in those supplemented with energy or ruminally undegradable protein. Houpt (1970) suggested that the transfer of urea N to the rumen may be limited and may approach a maximum under appropriate conditions. Urea transfer from blood to the PDV was likely near maximum for all dietary treatments in this study. The influence of large amounts of readily fermentable carbohydrate probably dominated the potential effects of differences in blood or ruminal urea and ammonia concentrations.

Total heat production, calculated by use of the equations of NRC (1985), were calculated as 2,495, 2,540, 2,681, and 2,469 kcal/d for the sheep fed the control, urea, SBM, and BFM diets, respectively. Heat produc-

tion, calculated from net oxygen uptake, of the PDV was 442, 393, 421, and 426 kcal/d; and of the liver, was 483, 502, 621, and 648 kcal/d for control-, urea-, SBM-, and BFM-fed sheep, respectively. Further calculation indicates that heat production of the PDV was 17.7, 15.5, 15.7, and 17.3% of total heat production, whereas heat production of the liver was 19.4, 20.1, 23.2, and 26.2% of total heat production with control, urea, SBM, and BFM diets. Heat production of total splanchnic tissues (PDV plus liver) was 37.1, 35.6, 38.9, and 43.5% of total heat production, respectively. Although these estimates are subject to several potential sources of error, they support previous reports indicating that splanchnic tissues are responsible for a high proportion of total-body heat production (Ferrell, 1988; Huntington, 1989; Eisemann and Nienaber, 1990). In addition, these observations suggest that energy use by the liver, as indicated by oxygen use (Table 3) or as a percentage of whole-body energy use, may be influenced substantially by N source.

Implications

These results suggest that N recycling plays an important role in the total N economy of ruminants fed high-concentrate diets. These results suggest that recycled N does not provide adequate soluble N to the rumen for maximal microbial growth when a high-concentrate diet is fed. Supplemental urea provides soluble N to support microbial growth, thereby increasing the amino acid supply to the animal. Additional amounts of amino acids may be provided to the animal by dietary proteins escaping ruminal degradation. However, supplementation with ruminal escape proteins will likely be of benefit to the animal only if provided after needs for ruminal soluble N have been met.

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